Viewpoints

Research frontiers for improving our understanding of drought-induced tree and forest mortality

Summary

Accumulating evidence highlights increased mortality risks for trees during severe drought, particularly under warmer temperatures and increasing vapour pressure deficit (VPD). Resulting forest die-off events have severe consequences for ecosystem services, biophysical and biogeochemical land–atmosphere processes. Despite advances in monitoring, modelling and experimental studies of the causes and consequences of tree death from individual tree to ecosystem and global scale, a general mechanistic understanding and realistic predictions of drought mortality under future climate conditions are still lacking. We update a global tree mortality map and present a roadmap to a more holistic understanding of forest mortality across scales. We highlight priority research frontiers that promote: (1) new avenues for research on key tree ecophysiological responses to drought; (2) scaling from the tree/plot level to the ecosystem and region; (3) improvements of mortality risk predictions based on both empirical and mechanistic insights; and (4) a global monitoring network of forest mortality. In light of recent and anticipated large forest die-off events such a research agenda is timely and needed to achieve scientific understanding for realistic predictions of drought-induced tree mortality. The implementation of a sustainable network will require support by stakeholders and political authorities at the international level.

Introduction

Forests cover *c.* 30% of the terrestrial surface of the globe and annually sequester *c.* 25% of the CO_2 emitted by human activities (Pan *et al.*, 2011). In forested regions, trees are the dominating vegetation and structure ecosystem patterns and processes from the stand level to entire landscapes. However, ongoing global warming, in concert with episodic droughts, heat waves and associated increased vapour pressure deficit (VPD; e.g. Dai, 2012), has been causing elevated levels of both chronic and acute stress often leading to tree mortality across large forested regions of the globe (Breshears *et al.*, 2013; Eamus *et al.*, 2013; Ruehr *et al.*, 2014). By contrast, recent studies suggest that

increasing specific humidity and elevated atmospheric CO_2 concentration may partially offset mortality risk from drought and elevated temperature (Liu *et al.*, 2017). Nevertheless, periods of drought and heat stress often interact with other forest disturbances like fire and windthrow (Brando *et al.*, 2014) and can significantly amplify the incidence and severity of biological disturbances such as outbreaks of damaging insects and diseases (Williams *et al.*, 2013). Hence a better mechanistic representation of the diverse processes that drive tree mortality under drought is needed to improve predictions of forest responses to projected climate changes (McDowell *et al.*, 2015b) and to assess the fate of forests in coming decades.

Tree death is a challenging issue (see Box 1; Franklin *et al.*, 1987) and a major thrust of research has investigated drought-induced tree mortality mechanisms, specifically testing whether trees die from hydraulic failure (HF), carbon starvation (CS), biotic attack or from an interaction of those factors (McDowell *et al.*, 2008). However, despite many investigations, it has become apparent that the current understanding of tree physiological responses to drought and heat remains quite insufficient and further background knowledge is clearly needed to generate realistic projections of forest mortality events under rapid climate change (Hartmann *et al.*, 2015). For example, we currently do not have a predictive framework to answer (1) which species will be more sensitive to a given drought at regional or global scales, (2) which individuals within a population will be more vulnerable, and (3) which quantitative thresholds of physiological parameters can be used to predict forest mortality under future climate scenarios. Simple physiological thresholds have been difficult to determine (Adams *et al.*, 2017) and lack of progress emphasizes that our current research agenda must be rethought. Furthermore, attempts to predict tree mortality at specific sites have been largely inconclusive and suggest major limitations in current models (McDowell *et al.*, 2013b), possibly due to a poor understanding of mechanisms of mortality at scales larger than the individual tree (Clark *et al.*, 2016).
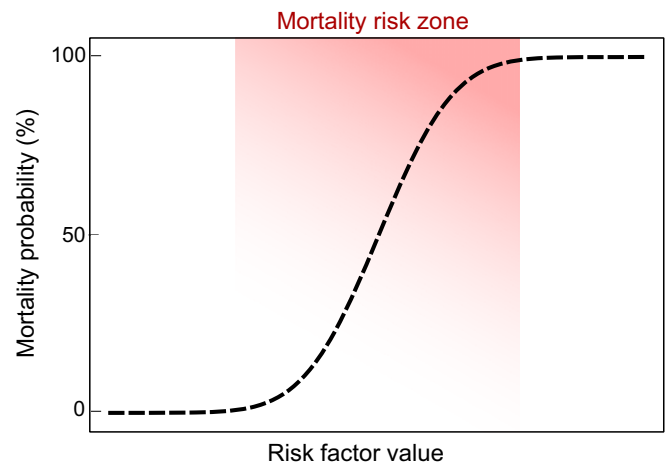
The complexity of tree mortality may greatly limit the generality and utility of physiological thresholds identified at the individual tree level for prediction at the population, landscape, regional or global levels. This implies, then, that physiological research at an individual scale might be most productive when identifying 'risk factors' that predispose trees to die, analogous in the human mortality literature to lifestyle factors such as smoking cigarettes that greatly increase the odds of death from a given cause like cancer (Sijbrands *et al.*, 2009). The identification of key functional and physiological risk factor traits, informed by the understanding of carbon (C) and hydraulic dynamics during tree death, has strong promise to improve our prediction of probabilistic mortality risk at the population level (Fig. 1).

Fig. 1 Conceptual representation of a probabilistic framework for predicting mortality of a tree population (e.g. species, plant functional type) based on risk factors. Ecophysiological research must determine thresholds for risk factors, e.g. xylem traits that are relevant for drought vulnerability/ tolerance, and beyond which the probability of mortality increases. The spread of the 'mortality risk zone' represents the variability of the risk factor with respect to occurring mortality. Different risk factors can interact, as when vulnerability to biotic attack increases with depletion of carbohydrates (McDowell *et al.*, 2011).

Box 1 Death is a complex issue in plants

A fundamental question in research on tree mortality concerns the underlying concept of tree death. While apparently intuitive, the concept of tree death is quite different from the concept of death in animals. In contrast to animals, plants lack a nervous system serving as a control organ and indicator of vital functions. In plants, meristematic cells maintain their capacity to differentiate throughout the life time of the plant and many plant cell types, even after their maturation, can re-differentiate, re-initiate cell division and, in some instances, reproduce whole organisms (Taiz & Zeiger, 2002). Meristematic tissues which can be found in stem and root apices and in the vascular cambium, allow trees to potentially grow indeterminately and to produce a modular body where organs/ tissues may die off without causing mortality of the entire tree (Klimešová *et al.*, 2015). Some tree species can survive thousands of years by creating hydraulically independent units that allow large tree parts to die back, while the organism itself survives (Larson, 2001).

A universal definition of tree death might thus be impossible to achieve. Instead, death indicators must be operationally defined at processes and scales meaningful to the scientific field, type of trees and research goals. Vegetation modellers may consider sustained periods of zero growth or the absence of aboveground living biomass (e.g. branches and stems) as mortality; while ecosystem ecologists may accept a high degree of defoliation at the canopy level in evergreen species (Galiano *et al.*, 2011; Guada *et al.*, 2016), and physiologists the absence of dark respiration (Hartmann *et al.*, 2013a) or mortality of cambial cells (Li *et al.*, 2016) as indicator of tree death. An alternative, potentially useful concept is the 'point of no return', when the organism is irreversibly prone to death although some tissues may still be alive. Several whole-plant metrics of the point of no return have been proposed, including loss of living aboveground tissue (quantified via leaf wilting and/or application of vital dyes to branch/stem tissues), cessation of water transport and hydraulic conductivity/water potential gradients that do not recover when conditions get wetter (Anderegg *et al.*, 2012).

Given the interdisciplinary character of tree mortality research, we must accept that an operational definition of tree death of a particular discipline will remain ambiguous to other disciplines. While being aware of the difficulty in translating this concept across disciplines, we urge here the need to clearly define and report criteria of tree death in individual studies while striving for more uniform definitions within each discipline and plant functional group (e.g. evergreens vs deciduous trees).

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identify crucial physiological risk factors in tree and forest mortality. Such risk factors can provide mechanistic relationships for more realistic predictions of future forest conditions.

Mechanisms of tree mortality

The hydraulic framework of global-change drought-induced tree mortality (McDowell *et al.*, 2008) proposed two nonexclusive physiological mechanisms: CS and HF. The relative importance and potential interaction between these two mechanisms leading to tree death has structured most of the research since this scientific debate was started (McDowell & Sevanto, 2010; Sala *et al.*, 2010). For this reason, we identify research frontiers mainly related to C and water relations as well as the role of biotic agents in tree mortality. In addition, the hydraulic framework emphasized ecological processes including plant resource acquisition, plant–biotic interactions and the ability of trees to recover from previous drought events. These topics, underrepresented in current research despite their potential significance in drought-induced tree mortality, are briefly discussed in Supporting Information Notes S1. Furthermore, some intrinsic factors known to influence tree responses to drought and heat, like tree functional type (Mitchell *et al.*, 2014; Ruehr *et al.*, 2016), developmental stage or age, are underrepresented in the current literature because most experimental studies so far have been conducted mainly on evergreen species and on individual potted tree seedlings or saplings (Table 1). This lack of information highlights the overarching research frontier of expanding future research on mortality-relevant functional and physiological traits to a larger range of tree species, developmental stages and functional types.

This synthesis is not intended as a reference for the 'state of the art' on drought-induced tree mortality understanding, as many recent reviews have already addressed challenges in predicting forest response to drought stress in detail (e.g. Allen *et al.*, 2015; Clark *et al.*, 2016). Here we identify key frontiers in drought-induced tree mortality research across different disciplines and scales, spanning physiological processes in individual tissues to assessments and predictions of local mortality events at regional to global scales. In addition, we provide research recommendations that serve as guidelines for directing future work to the areas of greatest need and update a global map of previously documented substantial mortality events (Fig. 2). We conclude by setting out a multidisciplinary strategy including practical recommendations that aim to
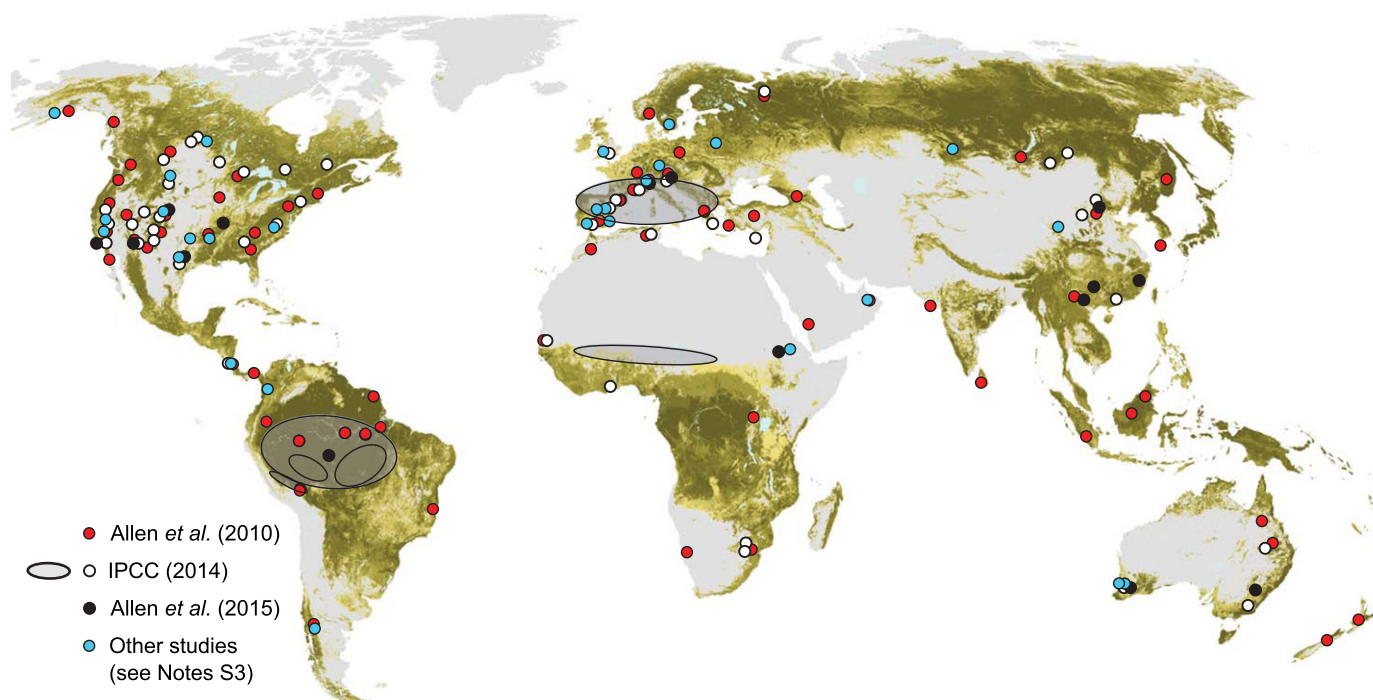
Fig. 2 Locations of substantial drought- and heat-induced tree mortality around the globe since 1970, documented by peer-reviewed studies, updated from Allen *et al.* (2015). Global forest cover (dark green) and other wooded regions (light green) based on FAO (2005). Studies compiled through 2009 (red dots) are summarized and listed in Allen *et al.* (2010); additional localities include the white dots and oval shapes derived from Figs 4–7 and its associated caption in IPCC (2014), the black dots from Fig. 2 in Allen *et al.* (2015), and additional localities (blue) from other recent publications listed in Supporting Information Notes S3.

Carbon

Support for CS is more ambiguous than for HF (O'Brien *et al.*, 2014; Sevanto *et al.*, 2014) and death from CS is still debated on (e.g. Körner, 2015) because complete depletion of C reserves is rarely observed. During water limitation, and in particular in combination with elevated temperatures and increasing VPD (Breshears *et al.*, 2013; Eamus *et al.*, 2013; Ruehr *et al.*, 2014), the net C balance of trees can become negative (Zhao *et al.*, 2013) and stored nonstructural carbohydrates (NSCs) must fuel respiration and several other vital processes, including osmoregulation (McDowell, 2011). Thus CS (defined here as the cessation of respiration) has to occur at nonzero NSC concentrations (Hartmann, 2015; Hoch, 2015). So far, however, many studies have addressed C dynamics during drought only partially, i.e. in individual tissues and/or organs. To systematically examine the role of tree C metabolism during drought mortality, we suggest investigating whole-tree C dynamics to identify the onset of a negative C balance during severe drought and in combination with high temperatures and high VPD. Such investigations must also address C storage mobilization and transport, regulation and remobilization of NSCs or alternative reserve compounds such as lipids and proteins during drought (Zhao *et al.*, 2013; Fischer *et al.*, 2015).

While the responses of photosynthesis to drought have been extensively studied, less is known about changes in whole-plant allocation patterns to C sinks including respiration, defence compounds, emissions of biogenic volatile organic compounds (VOCs), root exudates and export to symbionts (e.g. mycorrhiza,

rhizobia). VOC emissions (Loreto & Schnitzler, 2010) and respiration rates increase often with temperature (Adams *et al.*, 2009) but not always (Duan *et al.*, 2013) during drought. However, scarcity of data on these whole-tree processes currently limits our understanding of whole-tree C dynamics during drought-induced mortality. An important step forward would be to quantify the entire net C balance of trees to assess when C loss becomes larger than C uptake and available NSC reserves (see also the 'Interdependencies' section) and which minimum levels of NSC might become lethal (Weber *et al.*, 2018).

Water

Hydraulic failure has been addressed in many mortality studies (see references in Table 1) but the point at which xylem embolism develops into fatal HF for a large number of tree species is still unresolved (Urli *et al.*, 2013; Li *et al.*, 2016), and little is known about the different plant hydraulic strategies related to drought resilience. Therefore, a key research need is to determine specific thresholds of recovery and fatal embolism across individual tissues and whole plants.

Key features derived from xylem vulnerability curves that are generated under controlled conditions in the laboratory, including water potential (Ψ) leading to 50% loss in hydraulic conductivity (Ψ_{50}) possibly lethal in gymnosperms (Brodribb & Cochard, 2009) or 88% (Ψ_{88}) possibly lethal in hydraulically more tolerant and dynamic angiosperms (Urli *et al.*, 2013; Li *et al.*, 2016), have been suggested as potential indicators of HF

Table 1 Summary of published experimental studies on drought-induced tree mortality (Adams *et al.*, 2017) showing plant functional type (PFT), study type (field, glasshouse (GH), growth chamber (Cham) or outdoor potted (Out-pot)) and developmental stage of the trees used in each study

Species	PFT		Study type	Develop. stage	Reference
	Main	Alternate			
Acer pseudoplatanus	TBD		Out-pot	Seedling	Piper & Fajardo (2016)
Populus balsamifera	TBD	BBD	GH/Out-pot	Seedling	Galvez *et al.* (2013)
Populus tremuloides	TBD	BBD	Field	Mature	Anderegg *et al.* (2012)
Populus tremuloides	TBD	BBD	GH/Out-pot	Seedling	Galvez *et al.* (2013)
Eucalyptus globulus	TBE		GH	Seedling	Mitchell *et al.* (2013, 2014)
Eucalyptus radiata	TBE		GH	Seedling	Duan *et al.* (2014)
Eucalyptus smithii	TBE		GH	Seedling	Mitchell *et al.* (2013, 2014)
Nothofagus dombeyi	TBE		GH	Sapling	Piper (2011)
Nothofagus nitida	TBE		GH	Sapling	Piper (2011)
Callitris rhomboidea	TNE		GH	Seedling	Duan *et al.* (2015)
Juniperus osteosperma	TNE		Out-pot	Sapling	Anderegg & Anderegg (2013)
Picea abies	TNE	BNE	Out-pot	Sapling	Hartmann *et al.* (2013a)
Picea abies	TNE	BNE	Cham	Sapling	Hartmann *et al.* (2013b)
Pinus sylvestris	TNE	BNE	GH	Sapling	Garcia-Forner *et al.* (2016)
Pinus edulis	TNE		GH	Sapling	Adams *et al.* (2009, 2013)
Pinus edulis	TNE		Out-pot	Sapling	Anderegg & Anderegg (2013)
Pinus edulis	TNE		Field	Mature	Plaut *et al.* (2012)
Pinus edulis	TNE		GH	Sapling	Sevanto *et al.* (2014)
Pinus radiata	TNE		GH	Seedling	Duan *et al.* (2015)
Pinus radiata	TNE		GH	Seedling	Mitchell *et al.* (2013, 2014)
Pinus sylvestris	TNE	BNE	Field	Mature	Galiano *et al.* (2011)
Dryobalanops lanceolata	TrBE		GH	Seedling	O'Brien *et al.* (2015)
Durio oxleyanus	TrBE		GH	Seedling	O'Brien *et al.* (2015)
Hopea nervosa	TrBE		GH	Seedling	O'Brien *et al.* (2015)
Koompassia excelsa	TrBE		GH	Seedling	O'Brien *et al.* (2015)
Parashorea malaanonan	TrBE		GH	Seedling	O'Brien *et al.* (2015)
Parashorea tomentella	TrBE		GH	Seedling	O'Brien *et al.* (2015)
Shorea argentifolia	TrBE		GH	Seedling	O'Brien *et al.* (2015)
Shorea beccariana	TrBE		GH	Seedling	O'Brien *et al.* (2015)
Shorea macrophylla	TrBE		GH	Seedling	O'Brien *et al.* (2015)
Shorea parvifolia	TrBE		GH	Seedling	O'Brien *et al.* (2015)

References can also be found in Supporting Information Notes S2.
Details for PFT: TBD, temperate broadleaf deciduous; TBE, temperate broadleaf evergreen; TNE, temperate needleleaf evergreen; TrBE, tropical broadleaf evergreen; BBD, boreal broadleaf deciduous; BNE, boreal needleleaf evergreen.

(Choat *et al.*, 2012). However, variation in resistance to embolism may vary substantially within a single species over space and time (Anderegg, 2015) due to potential effects of plant development (young vs adult trees), seasonality (timing of drought), differences among tissues, life history (including air-seeding fatigue), hydraulic capacitance and – potentially – embolism repair. Finally, little is known about the levels of *in planta* xylem exposure to very low tensions and associated thresholds of massive HF, because measurements are typically conducted on excised branches or stem segments. Frequently applied vulnerability curves carry the risk of overestimating xylem embolism (McElrone *et al.*, 2012), therefore new nondestructive methods such as X-ray micro-tomography (Cochard *et al.*, 2015) or optical techniques (Brodribb *et al.*, 2016) may be promising avenues (Cochard *et al.*, 2015).

Plant traits linking wood anatomy to hydraulic properties such as wood density, pit membrane thickness between adjacent vessels and torus overlap in conifer tracheids may be useful proxies for embolism resistance (Li *et al.*, 2016). Given that some trees' hydraulic pathways may be highly segmented across organs (e.g.

Tyree & Ewers, 1991; Bucci *et al.*, 2012; Johnson *et al.*, 2016), emerging research should identify critical levels of water potential related to embolism and organ loss. A better mechanistic understanding can then be gained by quantifying the range from recoverable to lethal xylem Ψ and its native embolism to provide a probabilistic base for mortality estimates. This should then be linked to hydraulic traits in different tree species/functional types across forested biomes.

Interdependencies

Carbon and water dynamics in plants are ultimately interrelated via stomatal regulation and vascular transport. The interdependency of CS and HF in drought-induced tree mortality has been conceptually well established (McDowell, 2011) but investigations have only recently addressed this formally (e.g. O'Brien *et al.*, 2014). Several urgent mortality-related frontiers emerge: (1) establish how disruption of xylem–phloem functioning relates to CS, and (2) identify plant functional type-specific traits related to both CS and HF that can serve as risk factors in mortality predictions.

A better knowledge of C transport processes, i.e. transport via living cells in xylem and phloem, including the loss of interconnectivity between organs, represents a crucial step towards mechanistic understanding of mortality. Measurements of phloem flow in trees are challenging (Sevanto, 2014) and despite recent promising advances (Savage *et al.*, 2016) phloem failure has rarely been experimentally investigated in studies on tree mortality (Sevanto *et al.*, 2014). Modelling studies show that high xylem tensions may inhibit water inflow into the phloem during drought, potentially leading to phloem transport failure of NSCs from sources to sink tissues (Mencuccini & Hölttä, 2010) due to elevated viscosity and turgor collapse in the phloem (Sevanto, 2014). *In vivo* investigations on plants are needed to assess the importance of phloem failure in tree mortality. Furthermore, remobilization of stored carbohydrates, i.e. the hydrolysis of starch to sugars, during drought can be inhibited by limited water availability (Sala *et al.*, 2010) and may contribute to C transport failure. We thus emphasize the need to investigate the physiological limits of phloem transport and remobilization of sugars.

NSCs play an important role as osmolytes to maintain turgor and avoid desiccation as Ψ in plant tissues decreases with drought (Sala *et al.*, 2012; Salmon *et al.*, 2015). As xylem tension increases, sugars become an important component of xylem osmoregulation and for maintaining xylem water flow (Secchi & Zwieniecki, 2011). These functions may limit NSC availability for other critical metabolic processes (Sala *et al.*, 2012). To address this frontier, the minimum threshold of NSC concentration required for osmoregulation should be studied among different plant tissues, species/functional groups and environmental conditions. Finally, the plasticity of hydraulic and C-related traits with life history (e.g. prior exposure to drought) and the gene-by-environment controls on these traits are relevant to consider.

Insects and pathogens

Plant-damaging insects and pathogens can either kill trees directly as primary agents, or compound physiological stress as secondary agents of tree mortality. Outbreaks are often associated with drought and periods of higher-than-average temperatures (Desprez-Loustau *et al.*, 2006; Anderegg *et al.*, 2015b). These conditions can directly affect insect and pathogen fitness (e.g. reproduction, development, dispersal, mortality), as well as alter tree suitability and predisposition to attacks (e.g. substrate quality, defence capacity, attraction due to emitted VOCs). Together, both mechanisms determine damage severity and likelihood of tree mortality triggered by biotic agents during drought. Understanding feedback loops and complex interactions between host trees, biotic agents and environmental conditions is thus crucial for predicting tree mortality. In this context we highlight the following research frontiers: (1) determine temperature-related changes in insect/pathogen phenology that dramatically increase outbreak risk, and (2) identify tree-intrinsic risk factors and critical values for drought-mediated predisposition to biotic attacks.

Higher temperatures have been reported to facilitate insect and pathogen phenology, finally resulting in an increased outbreak risk (Bentz *et al.*, 2010; Jönsson *et al.*, 2011). However, such a positive relationship is typically nonlinear, species-specific, and constrained by distinct thermal upper and lower thresholds (Raffa *et al.*, 2015). Moreover, fitness effects of increased temperature are expected to be more pronounced at higher latitudes than in the tropics where species are typically closer to the edge of their thermal tolerance (Deutsch *et al.*, 2008). Cooperation among plant ecophysiologists, phytopathologists and entomologists has the potential to improve our empirical understanding of how gradual or extreme temperature changes affect different insect/pathogen populations, and how altered population dynamics can be linked to tree mortality across different ecosystems.

In parallel, drought stress can make host trees more susceptible to insect and pathogen attacks due to temporally reduced tree defence mechanisms (Anderegg *et al.*, 2015b). In conifers, decreasing carbohydrate availability and low Ψ during drought can limit the production of defensive oleoresin and the generation of hydraulic pressure in resin ducts, both needed to resist bark beetle attacks (Netherer *et al.*, 2015), whilst the emission of specific VOCs from trees attracting bark beetles is typically enhanced under drought and elevated temperatures (Kautz *et al.*, 2013). Thus, drought clearly promotes tree mortality by bark beetle attacks, whereas for defoliating and sap-feeding insects and pathogens this relationship is less evident (Desprez-Loustau *et al.*, 2006). Pathogens often critically rely on moisture, but could also benefit from reduced tree defence and an association with insects. Foliage feeders are negatively affected by drought-induced alterations in leaf physiology (e.g. toughness) and chemistry (e.g. carbon/nitrogen ratio (C : N)). Adequately addressing the complex interactions between positive and negative effects from different levels of drought stress and/or elevated temperature on both hosts and agents as well as differentiating potential causes of mortality (drought vs biotic agents) is challenging (Ryan *et al.*, 2015). A combination of finely designed controlled experiments could provide information on risk factors including tree C, water and nutrient balances that are critical for defence. Ideally, similarly designed experiments should be conducted across different agent species, host types and levels of drought severity to reveal tree defence strategies in relation to tree physiological status.

Process integration, scaling and modelling from tissues to the global vegetation

Predicting drought-induced tree mortality is especially challenging because it requires integrating processes that occur on temporal scales from seconds to decades and spatial scales from cells to continents (Fig. 3). Consequently, scaling physiological and ecological processes that influence the probability of mortality over large geographic areas is a major challenge that has to be addressed to predict future risks of regional and global die-off events. At larger spatial scales, mortality is inherently probabilistic and thus we focus here on how key physiological mechanisms and risk factors at the individual tree level can be scaled up to provide changes in the probability of mortality in a species, population, or region.
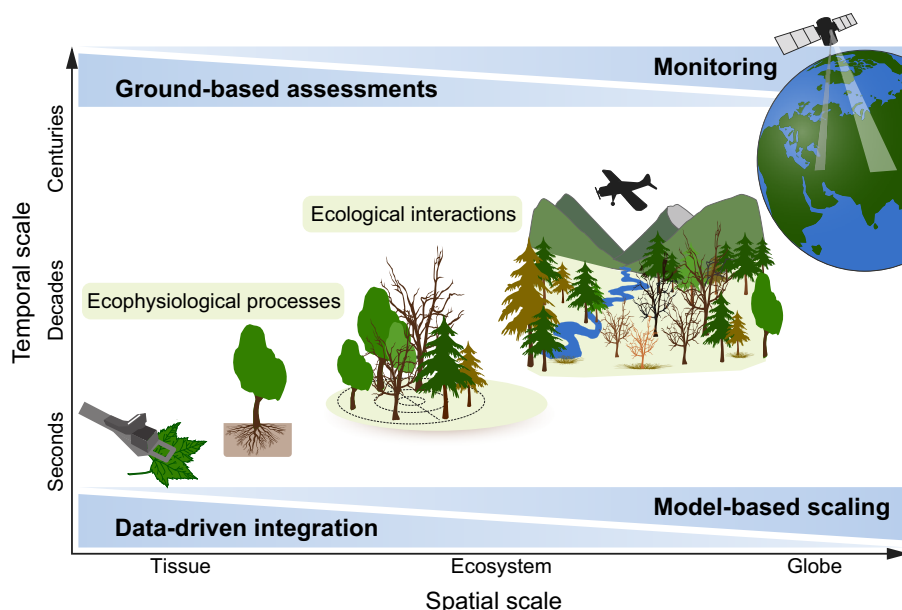
Fig. 3 Spatial and temporal scales of tree and forest mortality. Ecophysiological processes integrate over time and from tissue to tree level. These are further influenced by biotic and abiotic interactions at the ecosystem level and scale up to landscapes and longer time scales. A wide range of tools are needed for detecting, understanding and predicting tree death occurrences: while ground-based assessments provide data for process integration at smaller spatial scales, remote-sensing and large-scale monitoring are increasingly important for model-based global simulations and projections of forest mortality in future climate conditions.

Process integration and scaling issues in predictions of mortality

Scaling from individual trees to ecosystems and regions requires determining key environmental factors that may change the probability of mortality in space: (1) lateral water flows and the role of groundwater or hydraulic lift in mitigating water stress (Barbeta *et al.*, 2015), (2) existing spatial variation in soils, microclimate, and stand structure, and (3) biotic interactions that include insects/pathogens, and plant–plant interactions such as competition for water (see also Notes S1). For instance, landscape variability due to topography, soil characteristics, and management history likely promotes patchy patterns of mortality that are often observed across broad regions (Huang & Anderegg, 2012). The spatial pattern of tree mortality may be further affected by the interaction between drought and insect/pathogen outbreaks, due to the spatial nature of pest dispersal and infection (Anderegg *et al.*, 2015b). The contribution of such interactions to mortality distribution in space remains a crucial research area to inform simulations of mortality events.

Furthermore, mortality events must be considered within the timescales of tree population dynamics and contingencies of climate variations. For example, the sequence of mortality events and high growth periods experienced by tree populations is likely critical to determine long-term vegetation community dynamics. Positive feedbacks will increase forest vulnerability to new episodes of drought, if successive droughts lead to cumulative physiological damage, exhaustion of resources, diminished defence capacity and/or nonreversible loss of regenerating structures and recruitment capacity. Alternatively, stabilizing feedbacks may operate if tree mortality increases survival of neighbours due to competition release and adaptation of the forest community to drier conditions (Lloret *et al.*, 2012). Consequently, we highlight the following frontiers: (1) identify whether mortality probability of tree populations to

drought increases or decreases with successive exposure to stress, (2) determine the extent to which genetic adaptation and phenotypic plasticity mediate population resilience to drought and probability of mortality within a population, and (3) understand the impact of drought on population regeneration including seed production and recruitment.

Modelling

Models are important tools for integrating process understanding and making future projections across a gamut of spatial scales, ranging from individual trees to the entire globe (Fig. 3). We focus here on the integration of mortality processes in dynamic vegetation models (DVMs), particularly dynamic global vegetation models (DGVMs), although similar approaches and algorithms will be useful also in other model classes. There is currently considerable interest in improving the representation of tree mortality in DGVMs, given its importance on long-term forest dynamics (Bircher *et al.*, 2015), and in the regulation of ecosystem C storage (e.g. Friend *et al.*, 2014). However, tree mortality formulations in current DGVMs are generally simple, ranging from fixed C turnover rates (Galbraith *et al.*, 2013) to approaches where mortality is related to growth efficiency or negative C balance (McDowell *et al.*, 2011). Such approaches have been found to be insufficient to adequately capture observations of drought-induced tree mortality (e.g. Manusch *et al.*, 2012).

To address these problems, we identify the following research frontiers: (1) implement plant hydraulic representations in DVMs that allow for species-specific or plant functional type-specific drought strategies in dimensions of stomatal control, root distribution, allometry, and hydraulic properties such as vulnerability to embolism, (2) determine the key axes of drought trait trade-offs necessary to simulate different species' drought response strategies (Bartlett *et al.*, 2016) and how these are linked to probability of mortality (Anderegg *et al.*, 2016), and (3)
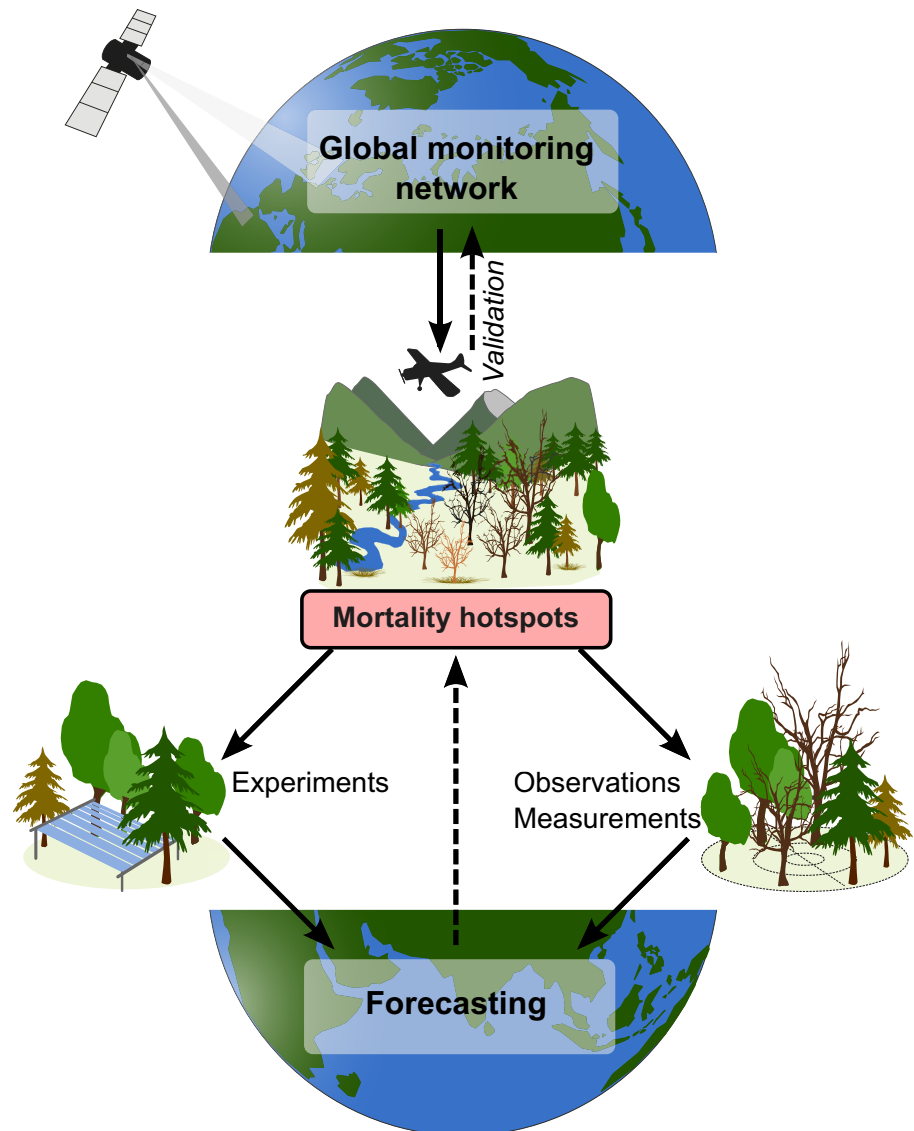
Fig. 4 Conceptual framework for focused research on drought-induced tree and forest mortality. A coordinated monitoring network that combines inventory plot data and satellite-based remote sensing can provide information on changes in forest cover and identify potential hotspots of mortality. Mortality occurrences in these hotspots can be validated using aerial-based remote sensing technologies like LiDAR. In these hotspots, investigations on the underlying physiological processes and ecological interactions through a combination of experimental manipulations and intensive field observations will provide mechanistic relationships allowing more realistic forecasting of forest conditions under anticipated future climate.

test and validate probabilistic mortality functions at regional scales against extreme droughts in the observational record where probability of mortality can be estimated through forest inventories, other plot data, or remote-sensing estimates (Brienen *et al.*, 2015). We emphasize that if mortality projections are made at regional scales, model validation against independent mortality data should be performed at the same spatial scales to have confidence in model projections.

Among these three research areas, simulating plant hydraulics is a key frontier for several main reasons. First, loss of hydraulic conductivity has been observed in almost every mortality event or experiment (Adams *et al.*, 2017). Second, thresholds in hydraulic loss have been documented in several species (e.g. Brodribb & Cochard, 2009) and hydraulic traits appear to predict which species in a community are at higher risk of mortality in a given drought (Anderegg *et al.*, 2016). Third, whole-tree hydraulic models exist and are relatively well-validated (e.g. Sperry & Love, 2015), suggesting they are suitable to incorporate into larger models.

Testing and validating mortality algorithms in DVMs is challenging. Standard mortality benchmark datasets are greatly needed, but have not yet been proposed. Many DVMs include only woody biomass pools and do not have explicit representation of 'trees' or at least tree cohorts that would be needed to calculate both drought hydraulic damage (e.g. embolism) and mortality rates to compare to plot-level data (McDowell *et al.*, 2013a). The nonlinear and threshold-like nature of probability of mortality will make the determination and calibration of thresholds for plant functional types difficult, especially for coarse functional types that are implemented in DGVMs. However, recent advances in synthesizing large-scale plot networks (Crowther *et al.*, 2015; Liang *et al.*, 2016) and remote-sensing (e.g. Hansen *et al.*, 2013) may allow assessment of thresholds at regional and larger spatial scales and for coarse groups of plants. Models that can accurately capture processes across spatial and temporal scales – ecophysiological dynamics, such as seasonal and inter-annual changes in Ψ and hydraulic conductivity, plot-level mortality rates, and regional plot

or satellite-estimated spatial and temporal patterns of mortality (Anderegg *et al.*, 2015a) – will be needed to improve confidence in mortality projections.

An integrative and multidisciplinary strategy for assessing, understanding and predicting future forest condition

In addition to the research frontiers and recommendations highlighted in the previous sections, we advocate here a comprehensive strategy towards a better understanding and forecasting of drought-induced tree mortality (Fig. 4; McDowell *et al.*, 2015a; Trumbore *et al.*, 2015) by including the following coordinated actions: (1) assess trends and hotspots in tree and forest mortality at the global scale via monitoring at multiple scales, (2) attribute mortality causes and drivers based on observations and manipulations in mortality-prone forest ecosystems and investigate the underlying physiological risk factors that may serve as mortality predictors that (3) allow then more realistic forecasting of forest responses to anticipated future climate such as changes in mortality probabilities with changing environmental conditions.

Assessing changes in forest condition via monitoring at multiple scales

Global forest health may be defined as 'a mosaic of successional [forest] patches representing all stages of the natural range of disturbance and recovery' (Raffa *et al.*, 2009, p. 815; Trumbore *et al.*, 2015) and may be best assessed by changes in forest condition spanning scales from trees to the globe (McDowell *et al.*, 2015a) thereby providing early warning indicators of forest stress (Allen *et al.*, 2010). The most robust and likely the most easily detected proxy for changes in forest health may be mortality rates that are outside of the natural range of variability (Trumbore *et al.*, 2015). In fact, many countries have excellent existing networks of detailed forest inventory plots that allow assessment of changes in forest condition because they are measured and revisited on a regular basis – many of these also include measures of tree mortality (e.g. in the United States, the Forest Inventory and Analysis Programme; Shaw *et al.*, 2005). However, these monitoring data are not available in 'real-time', are often not openly accessible and synthesizing data from multiple plot network sources (e.g. different countries) can be a complex task. In addition, historical inventory data typically have been field-collected on longer time intervals (commonly every 5–10 yr), making it difficult to pinpoint mortality occurrences to specific climatic events and/or causes of tree death. By contrast, satellite data are becoming more easily available and may allow 'close to real-time' assessments of changes in forest cover from disturbances over large regions (McDowell *et al.*, 2015a). Ground-based validation of satellite data may build on an already increasing number of inventory plot networks from both governmental agencies and/or multiple research institutions partnerships (like RAINFOR, FORESTPLOTS.NET or CTFS-ForestGEO) that cover different forest biomes. However, these plot-based monitoring networks were never designed to specifically address tree mortality, and we will need novel observation networks (or

protocols) that allow a faster and more automated detection of mortality events.

Recent advances in remote sensing provide a new generation of tools that could enable global satellite monitoring of die-off and other broad-scale disturbances (McDowell *et al.*, 2015a). For example, the Global Forest Watch initiative (http://www.global forestwatch.org) of the World Resources Institute is a good step forward to detecting temporal changes in forest cover from disturbance or mortality but the spatial resolution of the underlying data (30 m) is larger than the scale at which individual tree mortality occurs and precludes inferences on the underlying physiological processes. New technologies, like LiDAR, now allow monitoring of individual trees over larger areas (e.g. Asner *et al.*, 2016) thereby closing the gap between tree-level information from inventory plots and information at stand and regional scales derived from satellite data. The challenge now becomes to link these approaches in a coordinated manner, allowing (1) a direct flow of information between the different layers of monitoring, (2) a continued improvement of remote sensing products and an increase toward real-time mortality assessment and detection of mortality hotspots, and (3) a facilitated access to large international data sets to link ground-based and remotely sensed data (Trumbore *et al.*, 2015).

Although the Global Forest Watch provides 'close to real-time' information on forest conditions, changes in forest cover are currently captured by identifying areas with well-defined boundary attributes, like forest management and land-use change, or large-scale severe disturbances (e.g. wild fires, windthrow, insect outbreaks). Climate change-driven mortality of individual trees would thus likely appear as remaining spatially-diffuse changes in forest cover and are currently not systematically assessed. Such mortality should become a focus for ground-proofing via existing inventory or research plot data. Additional assessment cruises or LiDAR imaging will allow determination of whether changes in forest cover are due to mortality or reduced vigour of trees. Such measurements can be supplemented by multi-spectral imagery installed on UAVs (unmanned aerial vehicles, e.g. Dash *et al.*, 2017). Taken together such tools will open promising avenues to monitor forest health at scales relevant for detecting tree mortality (Hartmann *et al.*, 2018).

Understanding mortality causes and identifying mechanisms for forecasting: the roles of observations and experiments

To forecast drought-induced tree mortality we need to understand mortality mechanisms at the tree level first and use this understanding to derive mortality-related risk factors that allow probabilistic mortality predictions at larger scales. Naturally-occurring lethal drought events (identified as hotspots of spatially-diffuse mortality) detected by remote-sensing, may become platforms for intensive long-term observations, mid-term field manipulations and even close-up process studies of affected species under controlled environmental conditions such as in glasshouses (Fig. 4). Drought properties (duration, severity and timing of occurrence) that determine the physiological impact of water deficit on plants (Novák, 2009) have so far been almost completely neglected in drought mortality research and must be addressed in both field

observations and field/glasshouse manipulation studies. While observations and experiments on drought progression are still limited and hampered by the underlying complexity of defining drought (Paulo & Pereira, 2006), information gathered from naturally-occurring droughts can help improve experimental designs by focusing on more realistic combinations of drought characteristics along with increases in temperatures and VPD (Ruehr *et al.*, 2016). These drought characteristics (severity, duration, seasonality) can be manipulated in field and/or glasshouse or garden experiments to establish cross-species risk factors for tree decline and robust parameters for mechanistic relationships between changes in environmental conditions and tree physiological responses, especially if such investigations cover a range of regions and biomes (Adams *et al.*, 2017).

Although often limited to small trees, controlled and replicated experiments can provide insightful whole-tree perspectives on C dynamics including C flux measurements of gas exchange (photosynthesis and respiration), C allocation, NSC and non-NSC storage and remobilization (Ryan, 2011). An impressive attempt to study tree C balance responses in the field using whole-tree chambers has been recently demonstrated (Aspinwall *et al.*, 2016). Such studies combined with severe drought and heat treatments can provide unprecedented insights into mature tree C dynamics on the verge of death and hence indicate lethal NSC thresholds (Weber *et al.*, 2018) or minimum NSC thresholds required for osmoregulation. Studying such relationships in a large number of individuals and in several species or combining research efforts across similar designed experiments will provide probabilistic mortality distributions that help define the mortality risk zone (see Fig. 1).

Responses of a range of tree species and different functional types to different climate change scenarios, including elevated CO_2 and temperature with changes in VPD and specific humidity (Eamus *et al.*, 2013; Liu *et al.*, 2017), will provide information on the interplay of risk (e.g. high VPD) vs 'safety' (e.g. elevated CO_2) factors. Such studies are technically challenging and may be often limited to manipulation under controlled conditions (seedlings/ saplings) in the glasshouse, but attempts have been made to carry research into natural settings in the field and on larger trees (Aspinwall *et al.*, 2016).

In addition, observations and experiments along naturally-occurring drought and temperature gradients can be a valuable addition to drought experiments when studying tree responses to different climatic drivers (Stape *et al.*, 2006; Moore *et al.*, 2016; Binkley *et al.*, 2017) and interactions with nutrient limitations. Intensive field investigations will be most promising if common protocols for observations and measurements are developed and used across different projects (e.g. as in NutNet (https://nutnet. org), DroughtNet (http://wp.natsci.colostate.edu/droughtnet) and similar research networks). Impacts of insects and pathogens during drought must also become part of protocols in field studies and observations, as they are crucial risk factors in tree mortality.

Forecasting forest responses to climatic change

Scaling physiological and ecological processes that influence mortality over large geographic areas and implementing them in models is challenging. We posit that there are critical, high-priority steps for improving vegetation models' prediction of mortality: (1) model trees, and thus mortality, directly; incorporating individual-based representation of trees in DGVMs (e.g. Purves & Pacala, 2008) will enable direct simulation of tree mortality probabilities, rather than changes in biomass pools; (2) model hydraulics; incorporating tree-level hydraulics into vegetation models and scaling responses to regional scales that account for diversity in species, stand structures, and other sources of variation is likely to improve mortality predictions; (3) test mortality algorithms directly; more detailed and rigorous evaluation of mortality algorithms using plot networks and remote sensing products is greatly needed to test model simulations of mortality dynamics over large areas; and finally, (4) model NSC dynamics more realistically; like all sessile organisms, trees respond to environmental constraints by modifying resource (i.e. NSC) allocation to alleviate stress and compensate resource limitation. For example, plants are thought to increase root growth during drought to promote water uptake (*sensu* optimal partitioning, Poorter *et al.*, 2012). Although our knowledge of the regulation of NSC storage and remobilization in trees is still very limited (Hartmann & Trumbore, 2016) and accurate NSC measurements in plant tissues are still challenging (Quentin *et al.*, 2015), implementations of NSC dynamics in models that account for the perennial nature of trees will provide a more realistic prediction of tree responses to environmental change (Dietze *et al.*, 2014).

Conclusion

We provide a set of specific and crucial high-priority research frontiers that can help improve forecasting of forest conditions by promoting probabilistic mortality risk predictions. Similar to epidemiological research, mortality risk predictions for trees require also large data sets with substantial detail on the underlying physiological processes of the risk factors. This calls for international sharing of forest data and thus for a global monitoring network based on both governmental and academic support. Such a network will combine field observations, manipulations, controlled experiments and modelling. Although the central theme of this network will be based on data sharing, knowledge transfer to effective policy-making and forest management will become increasingly important for forest conservation. As most governments and concerned nongovernmental organizations (NGOs) have been acknowledging the central role of forests for human welfare and livelihood at the global scale, initiatives for forest monitoring should be ranked high up on the international political agenda.

Author contributions

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Notes S1 Mechanisms interacting with tree mortality: proposition for new key research areas.

Notes S2 References of published experimental studies on drought-induced tree mortality shown in Table 1.

Notes S3 Updated mapped reports of drought-induced tree mortality shown in Fig. 2.

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